
Nemacladoideae, a New Subfamily of Campanulaceae

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ABSTRACT. Data from morphology and sequencing of the chloroplast gene *rbcL* show that Cyphioideae (Campanulaceae) as traditionally circumscribed are not monophyletic. To remedy the situation, its genera are divided among three subfamilies, one of which, Nemacladoideae, is new.

The Campanulaceae as circumscribed by Cronquist (1981) included the genera sometimes segregated as Cyphiaceae, Cyphocarpaceae, Lobeliaceae, and Nemacladaceae, but excluded *Pentaphragma* Wallich ex G. Don and *Sphenoclea* Gaertner as distinct families. Recent phylogenetic analyses support the monophyly of this circumscription. In a recent study of sequence variation in the chloroplast gene *rbcL* (Cosner et al., 1994), exemplars of all five taxa formed a clade supported by 17 synapomorphies, with a bootstrap value of 100%, while exemplars for *Pentaphragma* and *Sphenoclea* fell in other clades. Basal to this clade was *Stylidium* Swartz ex Willdenow (Stylidiaceae). Their sister relationship was supported by only 12 synapomorphies, with a bootstrap value of 72%. A subsequent analysis of morphological data (Gustafsson & Bremer, 1995) likewise supported the monophyly of these five taxa and the exclusion of *Pentaphragma* and *Sphenoclea* from the clade.

The degree of phenotypic and genotypic differentiation evident among these five taxa is not excessive when compared to many other angiosperm families of comparable size. In the interests of consistency, therefore, it is deemed best to adopt Cronquist's circumscription of the family, and to consider Campanulaceae to incorporate all five taxa. The taxonomic structure that is evident in these data sets may then be expressed at subordinate levels of the hierarchy.

It has been traditional to divide a broadly circumscribed Campanulaceae into three subordinate groups, ranked as tribes (Bentham & Hooker, 1876) or more commonly subfamilies (Schönland, 1889; Wagenitz, 1964; Wimmer, 1968): Campanuloideae, Cyphioideae, and Lobelioideae. Although the monophyly of Campanuloideae and Lobelioideae found support in the molecular analyses (the morphological analyses scored each as a single exem-

plar), monophyly was not supported by either analysis for Cyphioideae. This possibility was first raised by Bentham (1875), who wrote (p. 6) "We have for technical convenience placed them [*Cyphocarpus*, *Nemacladus*, and *Cyphia*] together in a small third tribe intermediate between the two others [i.e., Campanuloideae and Lobelioideae]; but, strictly speaking, they may not perhaps form a truly natural group."

As noted previously (Lammers 1992), the Cyphioideae fall into three morphologically and geographically distinct groups: *Cyphia* in tropical and southern Africa; *Cyphocarpus* in northern Chile; and *Nemacladus*, *Parishella*, and *Pseudonemacladus* in western North America. The phylogenetic analyses based on both morphology and *rbcL* sequence data showed each to be an independent lineage within the clade here treated as Campanulaceae. Thus, the Cyphioideae as traditionally circumscribed are not monophyletic. To remedy this situation, the Cyphioideae are here divided into three subfamilies. Names are available for two, but the third requires a name. A key is provided to distinguish all five subfamilies, which are fully cited below. Note that if the traditional circumscription of Cyphioideae is retained, the name Cyphocarpoideae has four years' priority.

KEY TO THE SUBFAMILIES OF CAMPANULACEAE JUSSIEU, NOM. CONS.

- 1a. Corolla actinomorphic; odd (unpaired) sepal in a dorsal position; locules and stigmas (1–)3–5(–10)
..... Campanuloideae
- 1b. Corolla zygomorphic, sometimes only slightly so; odd (unpaired) sepal in a ventral position prior to any floral resupination; locules and stigmas (1–)2.
 - 2a. Flowers resupinate, the odd (unpaired) sepal in a dorsal position at anthesis; anthers connate, the dorsal 3 longer than the ventral 2
..... Lobelioideae
 - 2b. Flowers oriented normally, the odd (unpaired) sepal in a ventral position at anthesis; anthers distinct, all alike.
 - 3a. Corolla composed of a single cucullate dorsal lobe with an apical appendage plus 4 ventral lobes; stamens all epipetalous Cyphocarpoideae

- 3b. Corolla composed of 2 ± flat unappendaged ventral lobes plus 3 dorsal lobes; stamens epigynous or the dorsal two epipetalous.
4a. Perennials with tuberous roots; style tipped by a fluid-filled stigmatic cavity with a lateral pore . . . Cyphioideae
4b. Annuals (or if perennial, lacking tubers); style tipped by a bilobed stigma Nemacladoideae

Campanuloideae G. T. Burnett, Outl. Bot. 942, 1094, 1110. 1835, “Campanulidae.” TYPE: *Campanula* L.

Additional genera. *Adenophora* Fischer, *Asyneuma* Grisebach & Schenk, *Azorina* Feer, *Berenice* L. R. Tulasne, *Canarina* L., *Codonopsis* Wallich, *Craterocapsa* Hilliard & B. L. Burtt, *Cryptocodon* Fedorov, *Cyananthus* Wallich ex Bentham, *Cyclocodon* Griffith, *Cylindrocarpa* Regel, *Echinocodon* D. Y. Hong, *Edraianthus* (A. DC.) A. DC., *Feeria* Buser, *Githopsis* Nuttall, *Gunillaea* Thulin, *Hanabusaya* Nakai, *Heterochaenia* A. DC., *Heterocodon* Nuttall, *Homocodon* D. Y. Hong, *Jasione* L., *Legousia* Durande, *Merciera* A. DC., *Michauxia* L'Héritier, *Microcodon* A. DC., *Muehlbergella* Feer, *Musschia* Dumortier, *Namacodon* Thulin, *Nesocodon* Thulin, *Ostrowskia* Regel, *Peracarpa* Hooker f. & Thomson, *Petromarula* (Persoon) Ventenat ex R. Hedwig, *Physoplexis* (Endlicher) Schur, *Phyteuma* L., *Platycodon* A. DC., *Prismatocarpus* L'Héritier, *Rhigiophyllum* Hochstetter, *Roella* L., *Sergia* Fedorov, *Siphocodon* Turczaninow, *Theilera* E. Phillips, *Trachelium* L., *Treichelia* Vatke, *Triodanis* Rafinesque, *Wahlenbergia* Schrader ex Roth, *Zeugandra* P. H. Davis.

Nemacladoideae Lammers, subfam. nov. TYPE: *Nemacladus* Nuttall.

A ceteris subfamiliis Campanulacearum floribus non resupinatis, sepalo nongemino ventrali, corolla bilabiata lobis dorsalibus 3 et ventralibus 2, filamentis connatis distale, antheris distinctis, et stigmatibus bilobato differt.

Additional genera. *Parishella* A. Gray, *Pseudonemacladus* McVaugh.

Cyphioideae (A. DC.) Walpers, Ann. Bot. Syst. 2: 1037. 1852, “Cyphiaeae.” TYPE: *Cyphia* Bergius.

Cyphocarpoideae Miers, London J. Bot. 7: 61. 1848, “Cyphocarpaceae.” TYPE: *Cyphocarpus* Miers.

Lobelioideae G. T. Burnett, Outl. Bot. 942, 1094, 1110. 1835, “Lobelidae.” TYPE: *Lobelia* L.

Additional genera. *Apetahia* Baillon, *Brighamia* A. Gray, *Burmeistera* Triana, *Centropogon* C. Presl, *Clermontia* Gaudichaud, *Cyanea* Gaudichaud, *Delissea* Gaudichaud, *Dialypetalum* Bentham, *Diastatea* Scheidweiler, *Dielsantha* E. Wimmer, *Downingia* Torrey, *Grammatotheca* C. Presl, *Heterotoma* Zuccarini, *Hippobroma* G. Don, *Howellia* A. Gray, *Hypsela* C. Presl, *Isotoma* (R. Brown) Lindley, *Laurentia* Adanson, *Legenere* McVaugh, *Lysipomia* Kunth, *Monopsis* Salisbury, *Porterella* Torrey, *Ruthiella* Steenis, *Sclerotheca* A. DC., *Siphocampylus* Pohl, *Trematolobelia* A. Zahlbruckner, *Unigenes* E. Wimmer.

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